African Invertebrates 66(1): 133–150 (2025)
DOI: 10.3897/AfrInvertebr.66.138414

Research Article

Comparison of lowland tropical forest spider (Araneae) assemblages from Congo and Panama using a rapid assessment protocol

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Abstract

A Rapid Assessment Protocol (RAP) for non-canopy spiders was used to collect replicate samples from four lowland rainforest sites for a proof-of-concept comparison of spider assemblages from the Democratic Republic of the Congo (hereafter, Congo) and Panama. Collecting was done at two 0.25 ha sites in Panama and two 0.25 ha sites in Congo. At each site, three 0.01 ha plots were randomly located, and within each we did 1 person-hour of aerial sampling (sweeping and beating/brushing) and two person-hours of ground sampling (field sieving of leaf litter). The samples yielded 350 adult spiders belonging to 29 spider families. The Panama samples yielded more adult spiders (235 vs. 115) and more spider families (24 vs. 14) than the Congo samples. Overall, the dominant five spider families in these non-canopy samples were Theridiidae (24%), Salticidae (15%), Linyphiidae (11%), Oonopidae (10%), and Pholcidae (7%), with the 20 remaining families each making up less than 5% of the total adults. The three most abundant families in Congo were Theridiidae, Oonopidae, and Thomisidae, while the top three in Panama were Salticidae, Theridiidae, and Linyphiidae. An NMDS ordination analysis of the four plots failed to show significant differences between any of the four assemblages, but when the plots were analyzed by region, there was a significant difference in the family-level assemblages between the continents. This paper shows proof-of-concept that this RAP can produce statistically valid data from brief sampling trips by teams with inexperienced collectors and simple, inexpensive sampling equipment.

Key words: Afrotropical, family-level analysis, Neotropical, NMDS, Sampling

OPEN ACCESS

This article is part of:
Gedenkschrift for Prof. Stefan H. Foord
Edited by Galina Azarkina, Ansie Dippenaar-Schoeman, Charles Haddad, Robin Lyle, John MIdgley, Caswell Munyai

Academic editor: Caswell Munyai
Received: 2 October 2024
Accepted: 19 December 2024
Published: 19 February 2025

ZooBank: https://zoobank.org/A0EC36EB-46BE-4F28-B887-DD7D981BAAEE

Citation: Draney ML, Juakaly MJ-L, Sierwald P, Milne MA (2025) Comparison of lowland tropical forest spider (Araneae) assemblages from Congo and Panama using a rapid assessment protocol. African Invertebrates 66(1): 133–150. https://doi.org/10.3897/AfrInvertebr.66.138414

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Introduction

Comparing invertebrate faunas from different regions has historically proven to be problematic. Firstly, there is the significant taxonomic barrier of the necessity of knowing two disparate faunas, and the fact that there is often very little species overlap between very distant locations, and what overlap there is may be mainly due to the occurrence of widespread invasive or cosmopolitan species. These problems are largely alleviated by considering faunas at a higher

taxonomic level, as many spider families have very broad geographic distributions (Platnick et al. 2020; World Spider Catalog 2024). With spiders (Araneae), recent advances in molecular phylogenetic techniques (Coddington 2017) have increased our confidence that higher level taxa are monophyletic, allowing us to study disparate faunas at family level. The over 52,000 described spider species are currently placed within 134 spider families (World Spider Catalog 2024), and so the presence and abundance of these give us a way to compare the structure of spider assemblages in similar habitats across the planet. This approach is particularly valuable in studying the faunas of tropical rainforests, where the species tend to be poorly known and difficult to determine, and where many specimens within ecological samples may belong to undescribed species.

Even when this simplifying approach is used, our ability to compare faunas is very limited by the different ways in which the spiders are sampled. Whether examining carefully annotated regional species lists, or comparing faunas of particular sites with one another, the area sampled and the way the samples have been obtained can have significant effects on the resulting data. The species-area relationship, for example, is one of the best-known ecological principles (Connor and McCoy 1979), stating that larger areas have a very marked tendency to contain more taxa than small areas, and so two areas of very different size can be expected to vary in diversity even if they are very similar ecologically. The effect of sampling intensity on diversity is also very well known. Regions that have been intensively sampled, yielding vast numbers of individuals, will seemingly be more diverse than undersampled areas that have so far yielded only small numbers of specimens (Magurran 2004). Lastly, the methods used to sample animals obviously have a major effect on the species that are recorded (Samways et al. 2010), and so differences in two faunas could be due to different sizes of areas sampled, different intensity of sampling, and/or different methods of generating samples. If these factors are not kept constant, it makes comparison of even fairly well studied areas very difficult.

One solution to this problem that has emerged among community ecologists is the development of standardized sampling protocols. Several teams (for example, Scharff et al. 2003; Cardoso et al. 2008) have developed very robust sampling protocols to produce statistically comparable samples among sites, but the problem with these protocols generally is that they rely on very intensive sampling to produce a very thorough sampling of the site's fauna. They tend to use 1 ha as a plot size, which is a very large area to fully sample within a tropical rainforest (Draney personal observations). Unfortunately, most workers in tropical regions lack time and other resources needed to complete these very valuable surveys; they usually lack resources needed to access the canopy; and often it is unsafe to do fieldwork in the locations of interest at night, as recommended by many of these protocols. Therefore, most tropical sites have not (and probably will not) be sampled in this way, and yet environmental degradation of many sorts continues apace, and conservationists are in need of a way to quickly and cheaply obtain statistically sound, comparable data from which to base conservation prioritization and other management decisions.

A solution developed by Coddington et al. (1991) was an attempt to get comparable data from the existing practices of museum-based collectors, who often visit remote sites for short periods and do very intensive collecting. These methods standardize the collecting effort by constraining sampling time, so

that one sample would be the result of one collector using one method for one hour, for example. This allows for very quick collection of samples, and these samples are indeed statistically replicable, but the method does not specify sampling intensity (since museum-based collectors tend to collect as much as time will allow), which makes comparisons from different sites problematic. Also, the area sampled is not specified or controlled for, so researchers following the same protocol in very different sized areas may thus still end up with significant differences in diversity among sites that may or may not be due to faunal differences. Some researchers have responded by specifying a very large sample area (1 ha or more; Scharff et al. 2003; Cardoso et al. 2008) such that "complete" sampling isn't possible, and sampling intensity thus has a big effect on the resulting data. Dobyns (1997) showed that constraining sampling to a smaller plot size allows for more efficient collection of rare species and better estimation of richness on a smaller scale.

We have developed and are beginning to use a Rapid Assessment Protocol (RAP) that attempts to "thread the needle" between these two approaches (time and effort intensive, but thorough; versus efficient, but unconstrained with regard to plot size and sampling intensity), allowing researchers without sophisticated equipment to rapidly collect comparable samples of the ground-accessible portion of terrestrial ecosystems from randomly selected areas. These areas are always the same size and are sampled with the same amount of effort using the same sampling equipment, and so statistical comparison of samples should be possible. This paper represents our first attempt to compare the spider fauna of ecologically similar sites (lowland tropical rainforest) from two distant biogeographic regions, the Afrotropics (represented by two sites in the Democratic Republic of Congo) and the Neotropics (represented by two sites in Panama). The Panama sites were collected by a team of university students from the United States, visiting Panama on a travel course. They were mostly inexperienced collectors in an unfamiliar area, but supervised by an experienced field arachnologist. The Congo sites were also sampled by a team of mostly inexperienced Congolese university students, also supervised by an experienced field arachnologist. Both teams were limited in time (each site was sampled in 1–2 days) and equipment available: They each had to bring sampling equipment with them on arduous trips (transcontinental commercial air travel for the US students, and rented canoes and motorcycles for the Congolese students). In addition to giving us an interesting first comparison of the family-level spider communities of lowland rainforests of these two continents, we hope this paper also demonstrates the potential for using a RAP like ours to quickly obtain useful site-specific spider assemblage data, even with inexperienced and under-resourced research teams.

Material and methods

Study sites

We selected two complete sets of RAP data (described below) from two fairly mature lowland rainforest sites within nature preserves in each of Panama and D.R. Congo. Samples from both regions were collected in 1–2 days each during relatively dry seasons.

The Panama sites were located about 26 km apart; both are near the Panama Canal in the central area of the country at ca. 70 m a.s.l. Site "La Grua" is located near the canopy crane in Metropolitano National Park near Panama City (8.9941°N, 79.5440°W). It is a fairly mature, open rainforest. Being near the Pacific coast, it is drier than the following site. This site was sampled on 30 December 2007. Site "Rio Frijolitos" is located near the Rio Frijolitos crossing of Pipeline Road in Soberania National Park near Gamboa (9.1479°N, 79.7299°W). It seems to be a bit younger in successional age than the La Grua site, with more palms and smaller trees in the understory. Being on the Caribbean side of the continental divide, it receives somewhat more annual precipitation than the preceding site. The RAP samples were collected over the course of two days: 1 and 8 January 2008.

The Congo sites were both located in the Yoko Forest Reserve (0.2939°N, 25.2889°E), 34 km from Kisangani, which is ca. 450 m a.s.l., with an equatorial tropical climate. The temperature averages 25 °C with little monthly variation. There are two pronounced wet seasons, a minor one during March-May, and a major from September-December, peaking in October-November. The two Congo sites are less than 1 km apart, but have different forest types. The "*G. dewevrei*" site is a "monotypic" forest type, dominated by a single species of canopy tree, *Gilbertiodendron dewevrei* (Fabaceae). It was sampled on 13 August 2014. As the name implies, the "Mixed Forest" type is not dominated by this tree species, and features a higher diversity of canopy trees. This site was sampled on 21 February 2015.

Sampling: Rapid Assessment Protocol

All four sites were sampled using the same RAP developed by the first author (M. Draney) to enable a set of replicated, statistically comparable samples to be collected by a small team of collectors in a day or less, using simple and widely available equipment. Draney supervised a team of United States university students (with a few additional faculty) in Panama, and the second author (J-L. Juakaly) supervised a team of Congolese university students using the same protocol (but translated from English into French for the students' reference).

Sites to be sampled are not selected randomly; they are chosen because they are of interest to the researchers. But sampling locations within a site are randomly selected and located (process summarized schematically in Fig. 1). After a site is chosen, a marker/flag is placed on the ground at an arbitrary point on the roadside/trailside giving access to the site, and the GPS location is recorded for the site. Then, a 50 m transect is run along the trail, with markers placed at 0, 12, 24, 36, and 48 m. This serves as the "X axis" for the plot which has been arbitrarily placed in the study site. A compass is used to determine the direction that is perpendicular to this transect going into the study site (the "Y axis" of our plot). The "Y Axis" begins 24 m from the trail to reduce "edge effects" from the trail or road, so locations can be located 24, 36, 48, 60, or 72 m into the forest. Thus, the sampled sites consist of a ~ 50 × 50 m (0.25 ha) square located 24 m off the roadside, and it is sampled principally inside three 100 m^2 (0.01 ha) plots, with their centers being randomly selected pairs of X coordinates (0, 12, 24, 36, 48 m from the original trailside marker) and Y coordinates (24, 36, 48, 60, 72 m from the roadside). Three points are randomly located and flagged. If a point is too steep to sample, or contains a difficult or dangerous feature such as a streambed or a wasp nest, the point is discarded and a new random set of points is found.

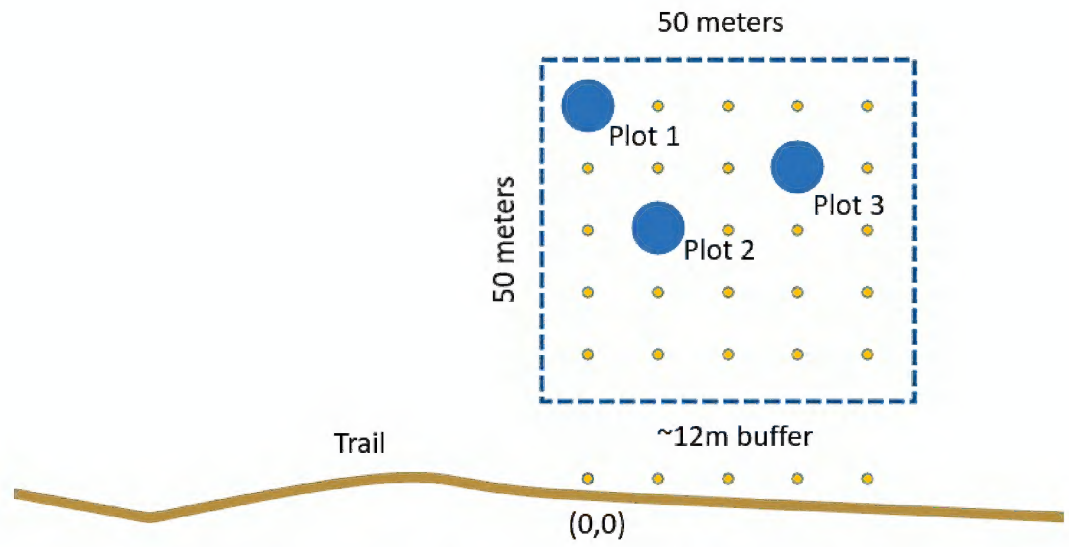

Figure 1. Spatial procedure of the Rapid Assessment Protocol. The thick line at the bottom of the figure represents a trail or road running through a rainforest of interest (blank space at top of figure). A site is demarcated by first flagging and getting coordinates of a spot on the trail (0,0). A tape measure run along the trail gives an X axis with flags at 0, 12, 24, 36, and 48 meters. A theoretical 0.25 ha (50 m x 50 m) plot located 12 meters from the trail in the rainforest has 25 points that can be randomly selected. They are reached by running a tape measure perpendicular to the X axis and flagging the center of the plot at the given Y axis distance. In the example, plot 1 is (0 meters, 72 meters); plot 2 is (12 meters, 48 meters), and plot 3 is (36 meters, 60 meters). At each selected point, a 0.01 ha (100 m^2) plot is constructed using a "compass rope" of the appropriate radius (5.64 m) to put flags and flagging around the circumference. In each plot, researchers collect an aerial sample (sweepnets, beating sheets) of 1.0 person-hour of effort, followed by a ground sample (litter sieving) for 2.0 person-hours of effort. See text for additional details.

A marker is placed at each of these three randomly selected points, which serve as the centers of three 0.01 ha (100 m^2) sampling plots. Each plot is surveyed by using a rope weighted at one end (for throwing to other workers) that is marked with the length of the radius of this 100 m^2 circle. About eight markers are placed around the circumference of each plot so that collectors can stay within the plot boundaries while sampling (Figs 2, 3).

After the plots are marked, they are sampled by small teams of collectors. They collect one person-hour of "aerial" method sampling, and two person-hours of "ground" method sampling. "Aerial collecting" focuses on spiders living in and on living and dead vegetation above ground level. The main sampling methods are sweeping with a canvas sweep net (Figs 4, 5a, b), and beating or brushing vegetation, tree trunks, etc., with a horsehair brush onto a 1 m^2 canvas or nylon beating sheet (Fig. 6a, b). Observed animals are aspirated or collected into collecting jars, then all animals are dispatched and stored in a solution of 50% propylene glycol and 50% water, labeled with the sampling information. Two collectors would collect for 30 minutes, four collectors for 15 minutes, etc. Normally, collectors paused the collecting (and the timing) midway through the sampling period. This allows for reorganization of collectors and their samples, and allows collectors to trade sampling equipment, so that a variety of collectors will use both sweep nets and beating sheets during each sampling bout. Collectors will also collect any spiders they see on vegetation or in webs during this time. A team of collectors are generally able to access all points inside the plots multiple times during the allotted sampling time.

The "ground" samples include hand capture of any spiders seen moving on the ground surface during the sampling time, but the main sampling method used is "high throughput litter sieving" using a ca. 35 cm diameter x 12.5 cm deep plastic geology test sieve (with ca. 9.5 mm openings; "Keene stackable poly sieve", Forestry Suppliers, Inc.). Leaf litter and associated material down to mineral soil is collected by quickly placing handfuls of litter (collected from

Figure 2. Visualization of the size of a 100 m^2 (0.01 ha) sampling plot, flagged out on a soccer field. The diameter of the circle is 11.28 m.

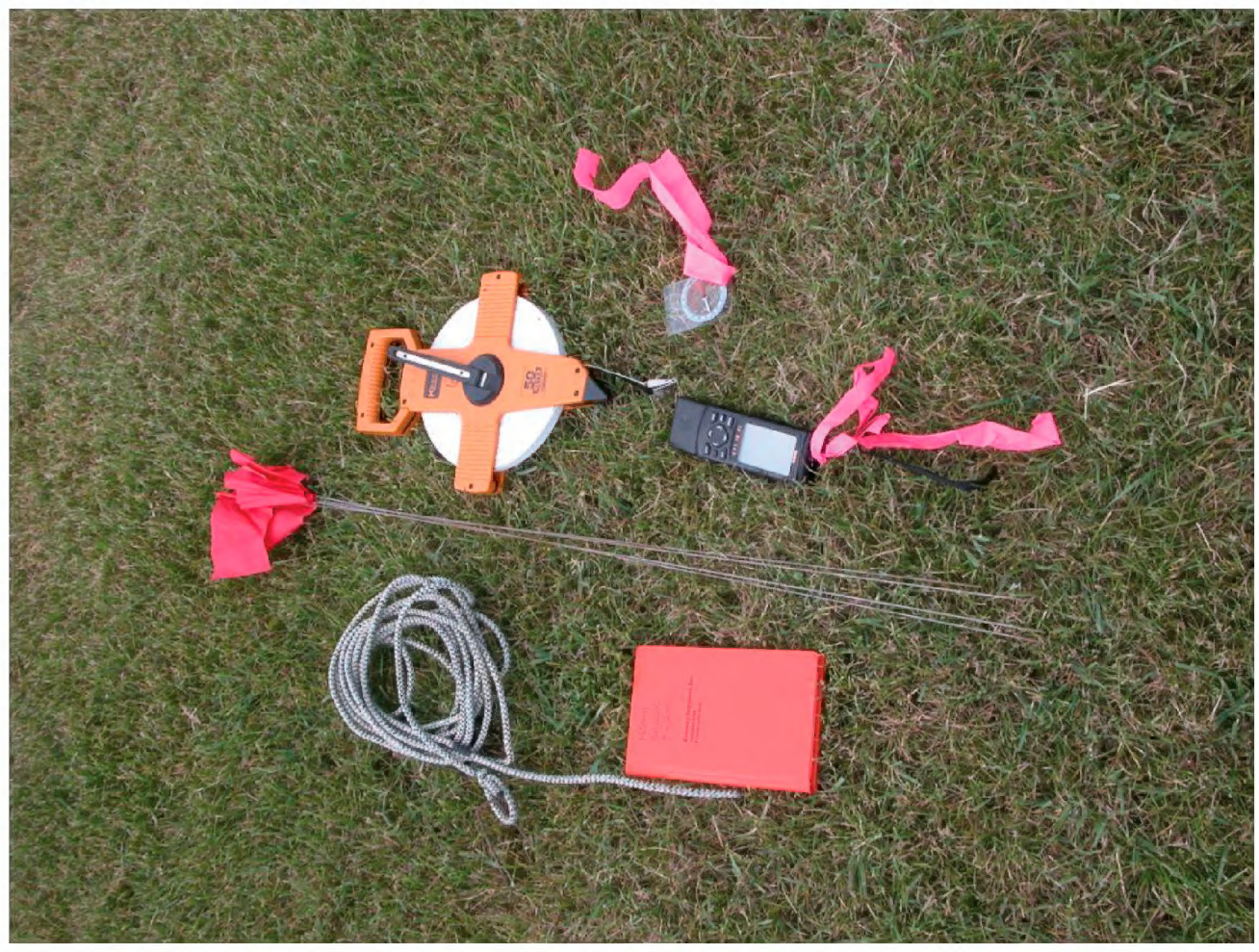

Figure 3. Simple equipment for surveying the RAP sample plots. Flags (and flagging) mark the plot center and boundaries, and mark out an X-Axis on the trail. A GPS unit (or smart phone app) can provide a accurate location of the plot origin. Tape measure and compass are used to find the random coordinates of the plot, and a compass rope (weighted at one end for throwing and marked for a radius of 5.64 m) is used to delineate the boundaries of three 0.01 ha sample plots within each 0.25 ha site. Details are recorded with pencil in a field book with waterproof paper.

throughout the 0.01 ha plot using gloves) into a plastic pail, and periodically dumping the collected material into a plastic sieve operated by another collector, who shakes the sieve onto a 1 m^2 nylon or canvas beating sheet laid on the ground immediately outside the plot (Fig. 7). Other collectors help by observing the sheet and collecting any observed spiders using collecting jars or an

Figure 4. Simple equipment used to sample spiders from the bottom ~2.5 m of the rainforest vegetation, referred to as an "aerial" sample. 1 m^2 nylon or canvas beating sheet catches spiders beaten or brushed from vegetation or tree trunks using a heavy dowel or a horsehair drafting brush. A canvas sweepnet is swept through the ground-layer vegetation. Smaller spiders are captured using an aspirator, whereas larger spiders are collected in a plastic jar. All spiders from one sample are killed and preserved in 50% propylene glycol in a Nalgene sample jar.

Figure 5. Students sampling a Congo and a Panama site using a sweep net and an aspirator (**a, b**).

aspirator (Fig. 8a, b). This is done for 2 person-hours (120 minutes) of effort. Any litter placed into the sieve before the timer ends is processed even after the timer goes off. Working in teams of 2–4, a group of collectors can process a significant fraction of the leaf litter in a 100 m^2 tropical rainforest plot within this time frame. As with the aerial samples, the animals collected in this way are preserved in a labelled jar with a solution of 50% water and 50% propylene glycol. The rationale for spending twice as much time sampling the leaf litter as the aerial vegetation is that the litter sampling is much less efficient yet eventually yields taxa not recovered in aerial samples. Evidence for this rationale is presented in the Results and Discussion, below.

Figure 6. Students sampling a Congo and a Panama site using a beating sheet, stick or drafting brush, and aspirator (**a, b**).

Figure 7. Simple equipment used to sample spiders from the ground layer of the rainforest. Wearing gloves, collectors rapidly put handfuls of leaf litter into a bucket, which is periodically transferred to a geology sieve. The sieve is shaken over the nylon beating sheet, and any spiders observed are collected using an aspirator, and the entire sample is transferred to a Nalgene sample jar preserved with 50% propylene glycol.

A third sampling method, lab sifted leaf litter, is used within the entire 0.25 ha site. These samples are collected in order to compare the data obtained by field sieving from the three 0.01 ha plots with litter collected from throughout the site and carefully sorted and sieved under laboratory conditions. Two 4-liter canvas geology sample bags are filled with handfuls of leaf litter collected by gloved collectors from anywhere they choose to go within the 0.25 ha site. As an additional control, one bag is collected by the principal collector (for example, M. Draney or J-L. Juakaly) and one bag is collected by one of the students (this was done to test whether collector experience had any effect on the samples; unpublished preliminary analyses using other data suggest there is no significant effect of collector experience). Each litter

Figure 8. Teams of collectors searching for spiders sifted from leaf litter at a Congo and a Panama site (**a, b**).

sample was carefully sieved by the team of collectors in the laboratory to try to obtain all spiders possible. As before, collected animals were preserved in 50% propylene glycol in pre-labelled containers.

Data analysis

After obtaining necessary export/import permits (see Acknowledgements) samples were shipped to the Field Museum of Natural History in Chicago, IL. The samples were washed using tap water on a 250 µm sieve and placed into

labelled glass containers in 70% ethanol. P. Sierwald (and Collection Assistant J. Louderman and museum volunteer J. Kase) identified all adult spiders to the family level using a variety of sources (Nentwig et al. 1993; Dippenaar-Schoeman and Jocqué 1997; Ubick et al. 2017). M. Draney examined vouchers of each family from each continent as a quality check on the spider identification. All material is housed in the Collection of Insects of the Field Museum of Natural History, Chicago. Only adult spiders were used in the present analyses to ensure accurate family-level identification of all animals.

In addition to tabulating the families recovered from each plot and method, we also used a species richness estimator (iChao1) to estimate the number of families likely to be accessible to our sampling at each of the four sampled sites (Chiu et al. 2014). These estimators work by comparing the number of taxa represented by exactly one individual (singleton taxa) with taxa represented by exactly two individuals (doubletons), three individuals (tripletons), and four individuals (quadrupletons), on the assumption that as sampling completeness is approached, singletons should make up an ever-smaller proportion of all taxa. We used frequency data for all RAP sample data from each site (all plots and methods pooled), and estimated iChao1 (with standard error and 95% lower and upper confidence limits) using the program SpadeR (Chao et al. 2015), with 100 bootstrap iterations.

In order to compare the family-level composition of the samples from the four sites, M. Milne did ordinations using non-metric multidimensional scaling analyses (NMDS, R 4.4.1). Prior to analysis, data were standardized by ln+1 transformations. Statistical significance between specific groups was determined using the pairwise.adonis package in R (Martinez 2017). Plots were created in R using the ggplot2 package and modified in Adobe Photoshop to remove color or replace colored points with greyscale ones.

For these analyses, ground and aerial samples from each of the 12 plots were combined to get total adult spiders collected per plot. Data from the site-wide lab-sifted litter samples were excluded from these plot-level analyses. Two ordination analyses were performed. Initially, we looked at each site independently (so each site consisted of replicate data from three plots). Since individual plots in the first analysis did not differ significantly (see Results), a second analysis was regional, comparing the Congo to the Panama plots. We again used the pooled plot data, but there were six plots per “region”.

Results

The RAP Samples from the four rainforest sites yielded a total of 350 adult spiders (Table 1), so an average of about 88 adult spiders per RAP sample set. However, about 2/3 of the adult spiders came from the Panama sites and 1/3 from the Congo sites (235 vs. 115). The Congo sites yielded 50 and 65 adult spiders, and the Panama sites yielded 103 and 132 spiders. From all four sites, spiders from 29 spider families (all Araneomorphae) were collected. The Congo sites yielded a total of 14 spider families (9 from the monotypic site and 14 from the mixed forest site) and the Panama sites yielded a total of 24 spider families (13 from the La Grua site, and 20 from the Rio Frijolitos site). Spiders in the family Theridiidae were most frequent in the samples, making up ~24% of adult spiders. Five families constituted over 2/3 of the adult spiders captured.

Table 1. Adult spider abundances and percent of site and total from the RAP sample sets from four lowland rainforest sites in Congo and Panama. The 29 sampled spider families are listed alphabetically.

Spider Family	Congo Monotypic Site	Congo Mixed Forest Site	Congo Total	Congo %	Panama Metro. Site	Panama Frijolitos Site	Panama Total	Panama %	Study Total	Study %
Anapidae	0	0	0	0	0	5	5	2.13	5	1.43
Anyphaenidae	0	0	0	0	1	0	1	0.43	1	0.29
Araneidae	4	3	7	6.09	0	7	7	2.98	14	4.00
Clubionidae	0	2	2	1.74	1	0	1	0.43	3	0.86
Corinnidae	0	2	2	1.74	0	5	5	2.13	7	2.00
Ctenidae	0	0	0	0	9	0	9	3.83	9	2.57
Deinopidae	0	0	0	0	1	3	4	1.70	4	1.14
Hahniidae	0	0	0	0	0	4	4	1.70	4	1.14
Hersiliidae	0	0	0	0	0	5	5	2.13	5	1.43
Linyphiidae	1	8	9	7.83	13	16	29	12.34	38	10.86
Mimetidae	0	3	3	2.61	0	0	0	0	3	0.86
Mysmenidae	0	0	0	0	0	2	2	0.85	2	0.57
Oonopidae	11	5	16	13.91	5	14	19	8.09	35	10.00
Oxyopidae	2	0	2	1.74	0	10	10	4.26	12	3.43
Palpimanidae	0	2	2	1.74	0	0	0	0	2	0.57
Philodromidae	0	0	0	0	1	0	1	0.43	1	0.29
Pholcidae	0	5	5	4.35	3	17	20	8.51	25	7.14
Pisauridae	0	0	0	0	12	0	12	5.11	12	3.43
Prodidomidae	0	0	0	0	0	1	1	0.43	1	0.29
Salticidae	5	3	8	6.96	25	19	44	18.72	52	14.86
Scytodidae	0	0	0	0	0	4	4	1.70	4	1.14
Sparassidae	0	0	0	0	0	2	2	0.85	2	0.57
Tetragnathidae	1	2	3	2.61	3	1	4	1.70	7	2.00
Theridiidae	19	23	42	36.52	27	15	42	17.87	84	24.00
Theridiosomatidae	0	0	0	0	2	5	7	2.98	7	2.00
Thomisidae	5	7	12	10.43	0	0	0	0	12	3.43
Trachelidae	0	0	0	0	0	1	1	0.43	1	0.29
Uloboridae	0	0	0	0	0	1	1	0.43	1	0.29
Zodariidae	2	0	2	1.74	0	0	0	0	2	0.57
Adult Spiders	50	65	115	100.00	103	132	235	100.00	350	100%
Spider Families	9	12	14		13	20	25		29	

After Theridiidae, these were Salticidae (~15%), Linyphiidae (~11%), Oonopidae (~10%), and Pholcidae (~7%), with the 24 remaining families comprising about 33.1% of the adults, and all of the remaining families each made up less than 5% of the total adult spiders sampled.

Table 1 also shows the pattern of occurrence of the 29 sampled families in each of the four sampled sites. Five families were found in all four RAP sample sets; these included four of the most abundant families (Theridiidae, Salticidae, Linyphiidae, and Oonopidae) plus one additional family, the Tetragnathidae. Four families were found only in the Congo samples: Thomisidae, Mimetidae, Palpimanidae, and Zodariidae. One family, Thomisidae, was found at both Congo sites, but not at Panama sites. Fifteen spider families were found within the Panama RAP samples, but not the Congo samples (see Table 1). Of these, two families (Theridiosomatidae and Deinopidae) were found at both Panama sites but not in the Congo samples.

As shown in Table 1, Theridiidae dominated Congo samples, with over 36% of all adult spiders; second most abundant in these samples was Oonopidae at ~14%. Interestingly, the third most abundant spider family in the Congo samples was Thomisidae (10.4%), a family absent from the Panama samples. The top five families were the same as for the pooled RAP rainforest data (Table 1), but in Panama, Salticidae were the most abundant adult spiders in the samples, making up 18.7% of the total. Theridiidae were second (~18%), followed by Linyphiidae (12.3%).

In Table 2, we show the iChao1 estimates and 95% confidence intervals for family-level richness at each of the sampled sites (all RAP data pooled). These results show there is no overlap between either the lower or upper confidence bounds of these estimates, implying higher family-level richness in Panama than in Congo. Note that the lower bound estimates are more accurate than the upper bounds (Chiu et al. 2014), and there is only a modest difference in them (Congo sites varied from 9–12, and Panama sites from 14–21 estimated families). The upper and lower confidence intervals together produced only a small overlap between the less family-rich Congo sites and the richer Panama sites.

Fig. 9 shows the results of the NMDS ordination (of adult spider distribution among spider families) of the four RAP sites; in other words, the ordination of spider assemblage composition. The figure shows that plots within a site always clustered near each other, and the plots within continents likewise ended up near each other. Note that the low number of replicates per site (three) precluded the production of 95% confidence interval ellipses surrounding the data from each site. The overall analysis was found to be significant ($p < 0.0001$), indicating significant differences among sites in total. However, a pairwise comparison of the sites revealed that no site was significantly different from any other site; p values were all equal to or greater than 0.1.

Because the sites were not found to be significantly different in this analysis, we pooled the data from each continent to examine the family-level composition of lowland rainforest spider assemblages from Congo versus Panama (Fig. 10). Note that this two-region comparison involved six replicate plots per region, enough to construct 95% confidence interval ellipses around the data from each region. The family-level spider assemblages of the two regions were found to be significantly different from each other ($P = 0.0021$). Fig. 10 shows that the plots within each region clustered in fairly linear sequences in the ordination space, with the Congo plots spread principally along the X axis and the Panama plots spread in a tight sequence along the Y axis.

Table 2. iChao1 Family-level richness estimation for each of the sampled sites. Total frequency data were used for the entire RAP dataset for each site (all plots and methods pooled). C.V. = Coefficient of Variation; F = Families; s.e. = Standard Error of the iChao1 estimate. Additional details in Methods.

	Congo: *G. dewevrei*	Congo: Mixed Forest	Panama: La Grua	Panama: Frijolitos
Total Adult Spiders	50	65	103	137
Observed Families	9	12	13	20
Dataset C.V.	0.97	0.966	1.088	0.806
iChao1 Estimated F	9.98	12	22.422	24.408
s.e.	1.839	0.765	11.552	4.051
95% Lower Estimate	9.088	12	14.441	20.951
95% Upper Estimate	19.882	14.342	74.59	40.428

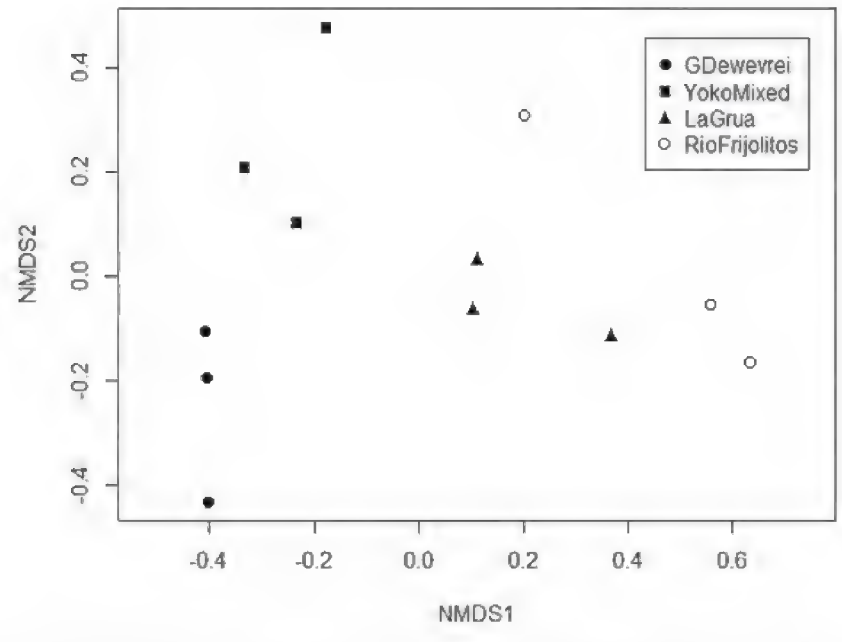

Figure 9. NMDS plot of among-site comparison of each of four sites separately. The two Panama sites are La Grua and Rio Frijolitos, and the two DR Congo sites are Yoko *G. dewevrei* monotypic and Yoko mixed species forest. Each data point represents distribution of adult spiders by family in one of three replicate 0.01 ha plots from each site, with ground and aerial data combined. The overall analysis was found to be significant ($p < 0.0001$), but no site was significantly different from any other site via pairwise comparisons ($p = 0.1$ was the lowest significance). A low number of replicates precludes the creation of 95% confidence interval ellipses.

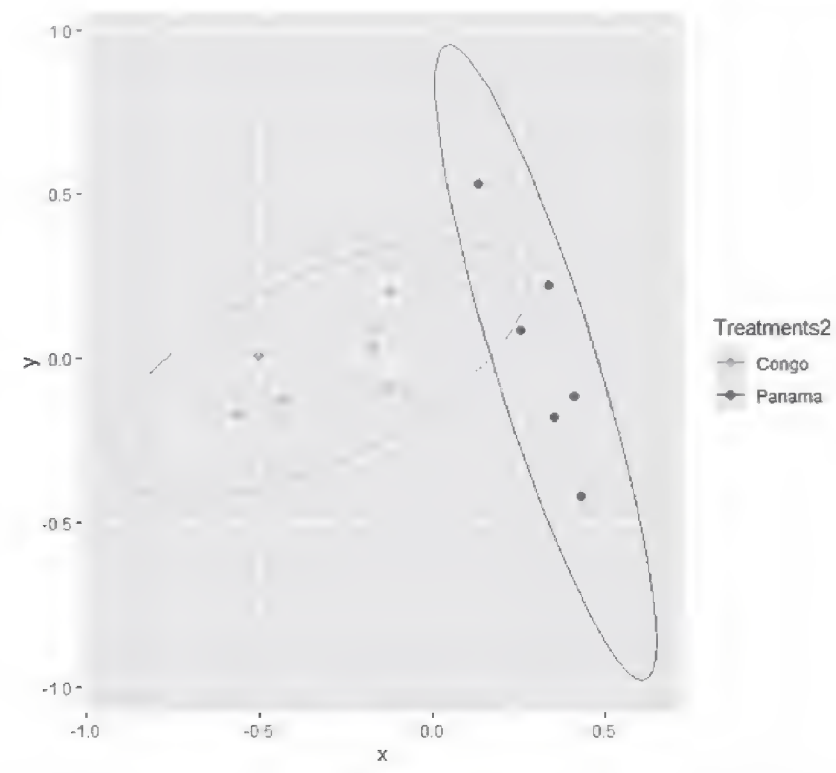

Figure 10. NMDS Comparison of plots from two biogeographic regions (Panama, Congo). Each region is represented by data from six replicate 0.01 ha plots. Each replicate consists of the pooled aerial + ground data, representing distribution of the adult spiders by family. The two regions were significantly different from each other ($p = 0.0021$) with little overlap in the predicted data ellipses, which represent 95% confidence intervals.

Table 3 shows the number of adult spiders and distinct spider families recovered from the aerial (sweepnet, beating sheet) and the ground (litter sieving) efforts in each plot of the dataset. The total Congo and Panama data show that both aerial and ground sampling yielded more spiders and families in the Panama sites than the same methods in the Congo sites. There may be a difference in effectiveness between the two regions, since both methods yielded similar spider numbers and families in Panama, yet in Congo the aerial samples yielded ~4 times more individuals and ~3 times more families than the ground samples did. The method totals (all sites pooled) showed that 1 person hour aerial samples yielded slightly more adult spiders than the ground samples (184 from aerial vs. 151 from ground), and that both recovered a similar number of spider families (20 from aerial and 21 from ground).

Table 3. Comparison of aerial (1 person-hour/plot) and ground sampling (2 person-hours/plot) methods among four rainforest sites. Three 0.01 ha plots were randomly located at each site, and one aerial sample and one ground sample was collected from each.

Nation	Site	Replicate Plot	Method	Adult Spiders	Families
D.R. Congo	*G. dewevrei* Forest	1	Aerial	7	4
D.R. Congo	*G. dewevrei* Forest	1	Ground	0	0
D.R. Congo	*G. dewevrei* Forest	2	Aerial	8	4
D.R. Congo	*G. dewevrei* Forest	2	Ground	0	0
D.R. Congo	*G. dewevrei* Forest	3	Aerial	20	4
D.R. Congo	*G. dewevrei* Forest	3	Ground	8	3
D.R. Congo	Mixed Forest	1	Aerial	26	9
D.R. Congo	Mixed Forest	1	Ground	5	2
D.R. Congo	Mixed Forest	2	Aerial	8	5
D.R. Congo	Mixed Forest	2	Ground	1	1
D.R. Congo	Mixed Forest	3	Aerial	13	6
D.R. Congo	Mixed Forest	3	Ground	7	2
Panama	La Grua Metropolitano	1	Aerial	7	2
Panama	La Grua Metropolitano	1	Ground	23	6
Panama	La Grua Metropolitano	2	Aerial	14	5
Panama	La Grua Metropolitano	2	Ground	17	7
Panama	La Grua Metropolitano	3	Aerial	18	6
Panama	La Grua Metropolitano	3	Ground	24	8
Panama	Rio Frijolitos	1	Aerial	16	12
Panama	Rio Frijolitos	1	Ground	16	10
Panama	Rio Frijolitos	2	Aerial	11	5
Panama	Rio Frijolitos	2	Ground	27	11
Panama	Rio Frijolitos	3	Aerial	36	9
Panama	Rio Frijolitos	3	Ground	23	7
Total, all Congo Aerial Samples (N = 6)				82	12
Total, all Congo Ground Samples (N = 6)				21	4
Total, all Panama Aerial Samples (N = 6)				102	16
Total, all Panama Ground Samples (N = 6)				130	20
Total, all Aerial Samples (N = 12)				184	20
Total, all Ground Samples (N = 12)				151	21
Total, all samples (N = 24)				335	28

Discussion

This study suggests that the ground-accessible spider assemblages of lowland rainforests from Congo and Panama may vary in several important aspects. The two Panama spider sites yielded more adult spiders, and more families of spiders were represented. Moreover, the family level structure of the assemblages (the families present and distribution of individuals among those families) was statistically different between the Panama and the Congo sites. Whether these differences are biologically significant, and whether they say something about the history and ecology of the respective regions, depends on the reasons for the differences of these assemblages.

The RAP controls for many variables that often cloud our ability to interpret differences between sites. The size of the sampled site, the size of the plots where the samples were collected, and the number of plots sampled were the same for all compared sample sets, and the sampling intensity was exactly equal at three person-hours per plot, with 2/3 of the time devoted to sampling the ground layer

and 1/3 of the time devoted to sampling the vegetation layer which is inherently easier and more efficient to sample, and yields more spiders and taxa per hour of sampling. Yet, the litter samples seem to access different taxa from the aerial samples, and so contribute significantly to the total numbers (M. Draney, personal observations). Table 3 shows that this built-in bias toward litter sampling was justified, in that twice as much litter sampling yielded a similar number of adult spiders (184 from aerial samples, 151 from ground samples), and a similar family level richness (20 families recovered from aerial samples, 21 families from ground samples). It seems that spending twice as much time on litter sieving may indeed optimize the information gained per unit of sampling time.

Of the between-site differences observed, adult spider abundance is likely the most variable and the least likely to be due to ecological differences between the sites. Although all four sites were sampled in relatively dry seasons, they were collected in different months, and so seasonality can impact the catch. Although all samples were collected when no rain was falling, the weather during the days and weeks before sampling can alter spider abundance. Spiders are more likely to be actively foraging during humid periods, for example (Draney personal observations), and this can impact the number of spiders encountered. We do not consider the differences in abundance to be strong evidence of actual differences in spider density between the regions, although that hypothesis remains to be tested.

Family richness, the second variable examined in this study, seems less prone to the vagaries of weather than abundance, but here the problem is the well-documented relationship between taxon richness and sample size (Magurran 2004). Both Panama sites yielded more adult spiders and more spider families than both Congo sites, but the higher number of individuals collected from Panama sites could at least partly account for the difference in family richness. Still, the large difference in Family-level richness (nearly twice as many families in Panama samples: 24 versus 14) did surprise us, and these data yielded iChao1 richness estimates that showed little overlap, giving additional support to the hypothesis that the Panama sites have higher family-level richness.

The composition of the spider assemblages (the identity of sampled families) is likely to reflect real differences among the sites, at least when comparing the most commonly encountered families. The greater dominance of Theridiidae and Thomisidae in Congo sites, and of Salticidae in Panama sites, is hard to explain as reflecting anything other than real ecological differences between the sites. However, it has to be kept in mind that our relatively small sample size (350 adult spiders among four sites) means that interpreting less frequently collected taxa is inherently problematic. Many spider families that are important parts of rainforest spider assemblages were not recovered in our samples. For example, Nentwig et al. (1993) lists Panamanian spiders from 33 families from habitats very similar to our sampling locations, so our samples failed to turn up representatives from at least 9 families, including all the Mygalomorph taxa. Likewise, a pitfall study of the Masako Forest Reserve near Kisangani (Juakaly and Jocqué 2021) yielded 918 adult spiders from 18 families from young and old successional forests. This includes 11 families not found in our Yoko samples (although our Yoko RAP samples turned up 7 families not recovered in the pitfall study). Many of the spider families missing from sites in our study undoubtedly occur there but were not collected due to relative rarity, or to undersampling of microhabitats such as the forest canopy, or Mygalomorph burrows. Five spider families in

this study are represented by single individuals (singletons; Table 1), and it might have been just as likely to have collected zero individuals of these families as one. Most of the spider families in our study have very wide distributions and have been recorded in both regions. Of the 29 spider families sampled in this study, only two are likely not found in both regions (Central Africa and Central America): Anyphaenidae and Mysmenidae (neither recorded from D.R. Congo; Mysmenidae known from one species from Rwanda: Dippenaar-Schoeman and Jocqué 1997; World Spider Catalog 2024).

The aspect of our data that is hardest to explain away and is most likely to reflect actual differences among the spider assemblages is the distribution of spiders among the sampled families, which was found to be significantly different between the two regions in our NMDS pooled analysis. The most dominant taxa in an assemblage have the biggest effect on the placement of plots in the NMDS ordination space, and proportional representation of dominant taxa is not likely to be much affected by sample size or any of the other factors (weather, etc.) discussed above. Thus, one result of our study that we take seriously is that the family-level spider distribution of Central African rainforest sites is considerably different in composition to that of Central American sites. The differences in the composition of the most abundant families (Table 1) gives an idea of the specific differences, which remain to be clearly delineated and explained by further research. As far as we know, this is the first time that assemblages (as opposed to national or regional species lists) of African and Central American spiders have been compared, and standardized assessment protocols such as the one used in this paper make such comparisons possible. Clearly, this study is too small in scope to make a definitive comparison of lowland tropical rainforests of the two regions. Many more sites would need to be included in a more definitive analysis, and ideally more would be known about the vegetation and history of the sites. For rainforest sites, information on the spiders of the canopy would ultimately need to be included; they are excluded from our RAP because of the difficulty and cost of accessing them. This preliminary study serves as a proof of concept that a carefully thought-out Rapid Assessment Protocol can enable statistically rigorous comparisons of spider assemblages using data collected in a short period of time by teams with inexperienced collectors using inexpensive supplies and equipment.

Acknowledgements

The authors have many happy memories of interacting with Dr Stefan H. Foord at the 2016 International Congress of Arachnology in Golden, CO. He is very much missed among our group interested in diversity and ecology of ground-dwelling spiders.

The Panama samples were collected during a Panama Travel Course trip in 2007–2008. Collectors included M. Draney, A. Choudhury, B. Howe, V. Medland, A. Wolf and a number of students from UW-Green Bay and from St. Norbert College, De Pere, Wisconsin: B. Butterfield, K. Corio, J. Goyette, B. Grasse, M. Harvey, C. Osman, A. Rick, J. Sundance, J. Watson, and C. Wepking. Andrew McKenna-Foster helped Draney to initially develop the Rapid Assessment Protocol. We thank Raineldo Urriola, Adriana Bilgray, Lil Camacho and the rest of the logistics support team at Smithsonian Tropical Research Institute-Panama for logistical

help with the trip and sampling, and R. Shuman Baquiran for help in importing the specimens to the USA for study. The Panama material was collected under permit SE/A-113-07 to Michael Draney, and exported out of Panama under scientific permit No. SEX/A-2-08 to Michael Draney. We thank the Field Museum of Natural History, Chicago, and especially museum volunteer James Case and Collections Assistant James Louderman, for initial family-level spider identification.

The Congo samples were collected by Mbumba Jean-Louis Juakaly and his students, mainly André Lofanga, Pascal Baelo, Steve Ngoie, Sylvie Kasienene, John Ngbangi, Vinny Kitenge, Jules Esongolo, Héritier Golo, and Drangozo. The Congo sampling and shipping were supported by a 2014 UW-Green Bay Grant in Aid of Research to Draney and Juakaly, and a grant from the Field Museum Africa Council to Sierwald and Juakaly, which also supported a trip to the FMNH for Dr Juakaly. The Congo material was exported out of DR Congo under Attestation de Transport de Materiel Scientifique No FS/VDR/M8/2014, FS/VDR/M6/2014, and FS/VDR/o4/2015 to Mbumba Jean-Louis Juakaly.

We thank Subject Editor Caswell Munyai, reviewer Charles Haddad, and an anonymous reviewer, whose comments greatly improved this article.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

Draney: Conceived of the project; led the Panama fieldwork; checked all spider identifications; Analyzed data; Primary author of manuscript. Juakaly: Led the Congo fieldwork; Secondary author of manuscript. Sierwald: Logistics and funding; organized spider identifications; Secondary author of manuscript. Milne: Data analysis and visualization; Secondary author of manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Cardoso P, Scharff N, Gaspar C, Henriques SS, Carvalho R, Castro PH, Schmidt JB, Silva I, Szüts T, De Castro A, Crespo LC (2008) Rapid biodiversity assessment of spiders (Araneae) using semi-quantitative sampling: A case study in a Mediterranean forest.

Insect Conservation and Diversity 1(2): 71–84. https://doi.org/10.1111/j.1752-4598.2007.00008.x

Chao A, Ma KH, Hsieh TC, Chiu CH (2015) Online Program SpadeR (Species-richness Prediction And Diversity Estimation in R). Program and User's Guide. http://chao.stat.nthu.edu.tw/wordpress/software_download/

Chiu CH, Wang YT, Walther BA, Chao A (2014) An improved nonparametric lower bound of species richness via a modified Good–Turing frequency formula. Biometrics 70(3): 671–682. https://doi.org/10.1111/biom.12200

Coddington JA (2017) Phylogeny and Classification of Spiders. In: Ubick D, Paquin P, Cushing PE, Roth VD (Eds) Spiders of North America: An identification manual. Second Ed. American Arachnological Society, 18–24.

Coddington JA, Griswold CE, Silva D, Peñaranda E, Larcher SF (1991) Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology, Vol. 2.

Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. American Naturalist 113(6): 791–833. https://doi.org/10.1086/283438

Dippenaar-Schoeman AS, Jocqué R (1997) African Spiders: An identification manual. Plant Protection Research Institute Handbook No. 9. Agricultural Research Council, South Africa, 392 pp.

Dobyns JR (1997) Effects of sampling intensity on the collection of spider (Araneae) species and the estimation of species richness. Environmental Entomology 26(2): 150–162. https://doi.org/10.1093/ee/26.2.150

Juakaly MJL, Jocqué R (2021) Resilience of epigeal spiders (Araneae) after clear-felling for agriculture in a Central African rainforest. Arachnology 18(8): 849–858. https://doi.org/10.13156/arac.2021.18.8.849

Magurran AE (2004) Measuring Biological Diversity. Wiley Publishing, Hoboken, New Jersey, 256 pp.

Martinez AP (2017) pairwiseAdonis: pairwise multilevel comparison using adonis. R package version 0.0.1. https://github.com/pmartinezarbizu/pairwiseAdonis [accessed 24 September 2024]

Nentwig W, Cutler B, Heimer S (1993) Spiders of Panama: Biogeography, investigation, phenology, check list, key, and bibliography of a tropical spider fauna. Flora and Fauna Handbook No. 12. Sandhill Crane Press, Gainesville, 227 pp.

Platnick NI, Hormiga G, Jäger P, Jocqué R, Ramírez MJ, Raven RJ (2020) Spiders of the World, A Natural History. Princeton University Press, Princeton and Oxford. 256 pp. https://doi.org/10.1525/9780691204987

Samways MJ, McGeoch MA, New TR (2010) Insect Conservation: A handbook of approaches and methods. Oxford University Press, 458 pp. https://doi.org/10.1093/oso/9780199298235.001.0001

Scharff N, Coddington JA, Sørensen LL, Griswold CE, Hormiga G, de Place Bjorn P (2003) When to quit? Estimating spider species richness in a northern European deciduous forest. The Journal of Arachnology 31(2): 246–273. https://doi.org/10.1636/0161-8202(2003)031[0246:WTQESS]2.0.CO;2

Ubick D, Paquin P, Cushing PE, Roth VD [Eds] (2017) Spiders of North America: An identification manual. 2nd edn. American Arachnological Society, 431 pp.

World Spider Catalog (2024) Version 25.5. Natural History Museum Bern. https://doi.org/10.24436/2 [accessed on 21–23 September 2024]